

Energy allocation strategies of young temperate fish: an eco-genetic modeling approach

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Abstract: We use an individual-based eco-genetic model to explore the relative selective pressures of size-dependent predation, overwinter mortality, and density-dependent energy acquisition in structuring plastic and adaptive energy allocation during the first year of life of a temperate fish population. While several patterns emerging from a suite of eco-genetic model simulations were consistent with past theoretical models and empirical evaluations of energy allocation by young fishes, results also highlight the utility of eco-genetic models for simultaneous consideration of plastic and adaptive processes. Across simulations, variation in genetic control of energy allocation was limited during very early ontogeny when size-dependent predation pressure was particularly high. While this stabilizing selection on energy allocation diminished later in the growing season, predation, overwinter mortality, and density-dependent processes simultaneously structured energy partitioning later in ontogeny through the interactive influence of plastic and adaptive processes. Specifically, high risk of overwinter mortality and low predation selected for high prioritization of energy storage. We suggest that simulations demonstrate the utility of eco-genetic models for generating null predictions of how selective pressures may structure expression of life history traits, such as early life energy allocation.

Résumé : Nous utilisons un modèle écogénétique basé sur l'individu pour explorer les pressions de sélection relatives de la prédation en fonction de la taille, de la mortalité durant l'hiver et de l'acquisition d'énergie en fonction de la densité sur la structuration de l'affectation plastique et adaptative d'énergie durant la première année de vie, dans une population de poissons de climat tempéré. Si plusieurs motifs qui ressortent d'un ensemble de simulations écogénétiques concordent avec des modèles théoriques et des évaluations empiriques antérieurs de l'affectation d'énergie par les jeunes poissons, les résultats font également ressortir l'utilité des modèles écogénétiques pour l'examen simultané de processus plastiques et d'adaptation. Sur l'ensemble des simulations, les variations du contrôle génétique de l'affectation d'énergie sont limitées durant le tout début de l'ontogénie, quand la pression de prédation en fonction de la taille est particulièrement forte. Si cette sélection stabilisante en ce qui concerne l'affectation d'énergie diminue plus tard durant la saison de croissance, la prédation, la mortalité durant l'hiver et des processus dépendants de la densité structurent simultanément le partitionnement d'énergie plus tard durant l'ontogénie par l'influence interactive de processus plastiques et d'adaptation. Plus précisément, un risque élevé de mortalité durant l'hiver et une faible prédation se traduisent par la sélection d'une forte priorisation du stockage d'énergie. Nous suggérons que les simulations démontrent l'utilité des modèles écogénétiques pour générer des prédictions nulles de l'influence potentielle des pressions de sélection sur la structuration de l'expression de caractères du cycle biologique, tels que l'affectation d'énergie au début de la vie. [Traduit par la Rédaction]

Introduction

Overwinter mortality is a strong selective force facing many temperate animals owing to extreme cold temperatures combined with low prey resource availability. As metabolism and energy stores scale allometrically with size (Kleiber 1932; Schultz and Conover 1999; Brown et al. 2004), small individuals are more likely to be adversely affected by overwinter conditions (Oliver et al. 1979; Post and Evans 1989; Hurst and Conover 2003). The relatively stronger impacts of winter on small individuals can lead to minimum size or total body energy thresholds for young animals to survive winter (Biro et al. 2005) and cause truncation of size ranges after winter because of higher mortality rates among smaller individuals (Biro et al. 2004; Garvey et al. 2004).

For temperate ectotherms, the survival benefits of both large size and high energy content at the onset of winter can lead to a

trade-off in allocation of energy. While overwinter mortality pressures may select for allocation of energy to storage tissues (e.g., lipid stores; Hurst and Conover 2003), other mortality sources may be strongly size-selective and only weakly related to energy stores. For example, young-of-year (YOY) fishes generally experience high rates of size-dependent predation early in ontogeny (typically in summer and early fall). As a result, YOY fishes may allocate resources to growth in structure (i.e., length) early in ontogeny when predation pressure is high and then shift to allocate energy to storage tissue as winter approaches (e.g., Hurst and Conover 2003; Mogensén and Post 2012). Such seasonal energy allocation has been observed for various fish species, including Atlantic salmon (*Salmo salar*) (Metcalf et al. 2002), largemouth bass (*Micropterus salmoides*) (Miranda and Hubbard 1994), striped bass (*Morone saxatilis*) (Hurst and Conover 2003), and yellow perch (*Perca flavescens*; Post and Evans 1989). The degree to which energy

Received 22 April 2014. Accepted 13 April 2015.

Paper handled by Associate Editor John Post.

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allocation varies seasonally may depend on a variety of factors, including winter duration and food availability (Mogensen and Post 2012).

Despite broad evidence of seasonal energy allocation among young fishes, elucidating mechanisms underlying energy allocation variation of young animals is complicated by diverse interactions among genetically fixed (adaptive) and environmentally plastic forces. Even after controlling for size and ontogenetic influences on energy apportionment, seasonal energy allocation may be genetically hardwired (Schultz and Conover 1997; Metcalfe et al. 2002; Hurst and Conover 2003). Further, over long time scales, local environmental conditions may select for distinct energy allocation patterns. It is well established that genetically controlled growth rates vary with latitude (e.g., Schultz and Conover 1997; Munch and Conover 2002). In the Northern Hemisphere, some northern fish populations express higher lipid content than southern populations (Berg et al. 2009). Thus, genetically controlled countergradient variation in growth (e.g., Conover et al. 1997; Munch and Conover 2002) may extend to influence not only latitudinal variation in growth in size, but also energy allocation. Simultaneously, plastic influences (e.g., seasonally variable temperature and food availability) may lead to seasonal variation in energy allocation independent of adaptively programmed provisioning. When fish acquire a high surplus of energy they are more likely to allocate a disproportionate amount of energy to storage tissue (Borcherding et al. 2007; Jacobs et al. 2012). Thus, even if prey resources are adequate to support positive growth, seasonal changes in availability and quality of prey may influence energy allocation and fish's body condition (e.g., Borcherding et al. 2007; Jacobs et al. 2012). Also, through influences on energy acquisition and metabolism, temporal changes in physiochemical conditions (e.g., temperature) can affect energy allocation patterns analogously to changes in prey (Byström et al. 2006).

While ecological and evolutionary processes have often been considered independently, various studies have highlighted how ecological and evolutionary processes interactively affect trophic interactions and life history trait expression (e.g., Heino and Dieckmann 2008; Palkovacs and Hendry 2010; Schoener 2011). The interaction of genetic and plastic processes have been acknowledged when considering patterns such as animal body size on islands (Palkovacs 2003) and responses to novel selection pressures, such as size-selective fisheries harvest affecting growth (e.g., Conover and Munch 2002; Wang and Höök 2009), maturity (e.g., Heino and Dieckmann 2008; Wang and Höök 2009), and ultimately natural mortality (Jørgensen and Fiksen 2010). Previous studies of life history adaptation show that energy allocation in YOY fishes can be both adaptive and plastic (Schultz and Conover 1997; Garvey et al. 2003), suggesting that studies of energy allocation under various selection pressures should consider both genetic and plastic processes.

Simultaneous influences of variable environmental factors and genetic controls complicate the ability to tease apart the influence of adaptive and plastic factors on seasonal or ontogenetic patterns in energy allocation. Moreover, optimal life history strategies may vary with population density and phenotypic composition (e.g., size; Metz et al. 1992). Thus, individual optimization models are often insufficient for predicting strategies, and instead agent-based models and game theory approaches (e.g., Maynard-Smith 1982) are more useful for predicting trait evolution under density- or frequency-dependent regulation. Eco-genetic models (Dunlop et al. 2009) offer a means of evaluating how selective environments may interactively structure both plastic and adaptive traits of model populations. Eco-genetic models build on individual-based modeling approaches (e.g., Dunlop et al. 2007, 2009; Wang and Höök 2009) to incorporate detailed information on species biology and ecology with inherited information. In general, the objective of eco-genetic models is not to recreate evolution but rather to function as dynamic genetic algorithms to select for

appropriate parameter traits for distinct environmental conditions. Eco-genetic models are beneficial because they track changes in parameter trait distributions without imposing predefined fitness functions (Dunlop et al. 2009) and allow for the influence of density-dependent processes on trait selection. Diverse eco-genetic models have been used to track changes in a variety of life history traits (e.g., size and age at maturation; Dunlop et al. 2009; Wang and Höök 2009).

Past studies have used a variety of approaches to model and empirically evaluate seasonal energy allocation patterns by young fishes (e.g., Schultz and Conover 1997; Post and Parkinson 2001; Huss et al. 2008; Mogensen and Post 2012). However, to our knowledge eco-genetic models have not been applied for this purpose. Eco-genetic model predictions can be viewed as null models for anticipating how selective pressures may structure expression of life history traits (Dunlop et al. 2007; Wang and Höök 2009) and have the advantage of simultaneously considering how both genotypic and phenotypic expression may respond to selective pressures. Thereby, applications of such models may either corroborate or contradict observations and predictions from previous studies and models, and we suggest they are analogous to dynamic genetic algorithms for generating null model predictions. Herein, we describe an eco-genetic model to explore how various selection pressures influence plastic and adaptive traits to structure energy allocation of YOY yellow perch in Saginaw Bay, Lake Huron, USA.

Model description

The model description follows the ODD (Overview, Design, concepts, Details) protocol (Grimm et al. 2006, 2010), which has been proposed to describe individual-based models.

Purpose

We applied an eco-genetic model to evaluate how size-dependent predation, overwinter mortality, and density-dependent growth acting on both adaptive and plastic processes alter YOY yellow perch energy allocation.

The model tracks generations of yellow perch experiencing various selective forces for 200 years in Saginaw Bay. While the model framework could be used to explore energy allocation patterns of many YOY temperate ectotherms, we use yellow perch in Saginaw Bay, Lake Huron, as a model population as (i) the physiology and ecology of yellow perch are well described, (ii) annual fall trawl surveys by the Michigan Department of Natural Resources provides many parameters specific to Saginaw Bay, and (iii) perch experience size-dependent overwinter mortality (Post and Evans 1989; Fitzgerald et al. 2006). Further, yellow perch in Saginaw Bay have recently experienced poor early life growth and survival (Ivan et al. 2011), and insights to energy allocation strategies of this population may inform early life dynamics. Recent studies have documented seasonal and ontogenetic energy patterns of young yellow perch in Saginaw Bay (Pothoven et al. 2014; Roswell et al. 2014). Ultimately, by parameterizing the eco-genetic model for a specific population, model behavior is grounded in reality; however, the implications and results from the model can be extrapolated to various temperate animal populations that experience size-dependent predation and overwinter mortality.

Entities, state variables, and scales

While total duration of simulations is flexible, we initially consider 200-year simulations. Since it is necessary to use a subannual time step to assess seasonal energy allocation (McNamara and Houston 2008), dynamics of YOY fish are described on a daily basis (from hatch to the end of the growing season on simulation day 305). Given the model focus on YOY fish energy allocation, age-1 and older fish are tracked on a coarser, annual basis. To reduce computational time, the model does not track single individuals; rather the model tracks super-individuals (SI; Scheffer et al. 1995), each of which represents variable numbers of individ-

uals. Additional state variables for each SI include total mass (g), length (mm), storage mass (g), structural mass (g), sex, maturity status, age, and 12 inherited energy allocation parameters.

The spatially homogenous thermal (°C) environment is updated daily. Temperature strongly influences potential daily energy acquisition and growth in ectotherms. Daily temperature (T_d) is assumed to remain ≥ 1 °C and vary seasonally based on Saginaw Bay temperature data from Johengen et al. (2000) as

$$(1) \quad \text{temp}_d = 0.0016d^2 - 0.6803d - 50.281$$

$$(2) \quad T_d = \text{MAX}(\text{temp}_d, 1)$$

where d is the simulation day.

Processes, overview, and scheduling

Simulations initiate with adult yellow perch (100 000 SIs from age-1 to age-9; Fig. 1). On day 100 of each year, adult maturation is assessed and mature perch reproduce and new YOY SIs are added to the model, with energy allocation parameters derived from their parents. Adults are assessed for growth and survival and their age is incremented, after which, adults are not assessed until reproduction the following year. Newly produced young perch are tracked on a daily basis. After hatching, YOY perch acquire energy, grow, and experience predation and starvation mortality. On the final day of the year, YOY potentially experience overwinter mortality. Then, young fish that survive winter become age-1 adults and are henceforth assessed on an annual basis.

Design concepts

Basic principles

Our eco-genetic model relies on established bioenergetics theory for fish growth and on inherited energy allocation parameters for seasonal energy allocation.

Emergence

Key outputs that emerge from this eco-genetic model are the population mean and variance values of the genetic traits controlling energy allocation in YOY perch, population abundance, and the percentage of mass allocated to storage tissue by YOY fishes.

Adaptation

Individuals are identical at hatch, with the exception of their inherited energy allocation parameters. On a daily basis, these parameters interact with individual energy acquisition to influence relative growth rates of storage and structural tissue, which in turn influence total growth rates and mortality risks. While individual energy allocation parameter values are fixed throughout an individual's life, at a population level, the relative frequency of inherited parameter values is free to change (e.g., evolve) over time.

Objectives

Individuals with energy allocation parameter values that promote survival and growth are more likely to successfully reproduce and pass on these parameter values to subsequent generations (i.e., their fitness will be relatively high). Suitability of energy allocation parameter values will presumably vary among different selection regimes. In short, individuals do not explicitly make decisions to increase or decrease their fitness, but selection pressures should select for appropriate parameter values which enhance relative fitness.

Learning, prediction, sensing

There is no explicit learning, prediction, or sensing by individuals in our eco-genetic model.

Interaction

Agents (individual YOY yellow perch) interact indirectly in simulations via exponential density-dependent competition for food. Moreover, adults interact during reproduction as traits of other adults influence relative reproductive success of reproducing individuals (see section on Age-1+ reproduction).

Stochasticity

Stochastic processes affecting YOY fish include individual mortality (predation, starvation, and overwinter) and energy acquisition. Energy acquisition and YOY size are modeled stochastically because (i) daily individual consumption is randomly assigned from a uniform distribution around a population mean and (ii) assigned genes controlling individual energy allocation are randomly assigned at initiation of the model and randomly passed on from parent to offspring. Stochastic processes affecting adults include annual mortality (10% variation from a random normal distribution) and growth in length (25% variation from the expected length using eq. 3). During reproduction, reproductive success of adults is modeled randomly, with larger SIs and SIs representing more individuals being more likely to reproduce successfully (based on the proportion of eggs or milt an SI contributes to the total egg or milt production). Assignment of individual sex and inherited parameter values of offspring are also stochastically assigned.

Collectives

Individuals do not interact as collectives.

Observation

At the end of each model year, a variety of population summary information is output. These results include the population mean, variance, minimum, and maximum of the following: total abundance, YOY abundance, YOY length, YOY total mass, YOY storage mass, and inherited energy allocation parameters.

Initialization

We calibrated the initial baseline simulation such that the size range of YOY yellow perch at the end of a simulation year was similar to sizes observed in Saginaw Bay (Ivan et al. 2011). The model initiates with 3 million individuals represented by 100 000 SIs. At hatch, YOYs are always represented by 10 000 SIs. Adult state variables are randomly assigned for sex and the values of 12 energy allocation parameters (initial values uniformly distributed from -0.2 to +0.2). Age is assigned randomly to each SI proportional to fall trawl catch data from Saginaw Bay for 1986–2004 (Fielder and Thomas 2006), and length is assigned based on sex-specific von Bertalanffy equations derived from Jackson et al. (2008) with random variation. Maturation is determined based on fish length at age, while mass is assigned based on a length–mass regression.

Input data

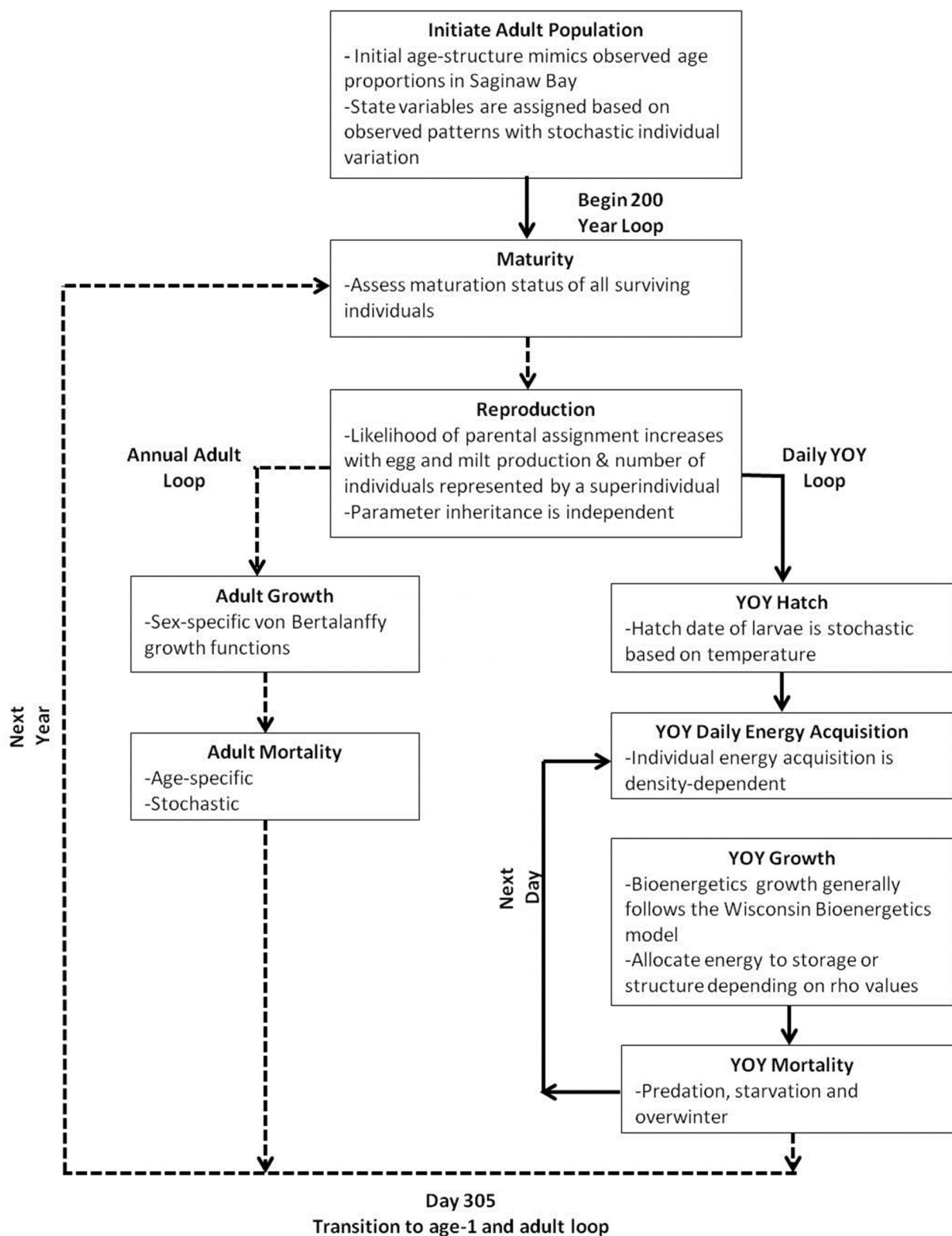
No additional input data are required for the model. However, model response is considered among simulations with altered selection pressures (size-dependent predation mortality, overwinter mortality, and density-dependent effects) and inheritance structure (see below).

Submodels

Age-1+ maturation, growth, and survival

As the model focuses on energy allocation of YOY SIs, we do not track growth and survival of adults on a daily basis. Adult SIs essentially serve as reservoirs for genetic traits, but their potential contributions to subsequent generations varies throughout life (as abundance and body size change). Three processes are considered annually for age-1+ fish: maturation, growth, and survival.

Fig. 1. Flow diagram for the eco-genetic, individual-based model of young-of-year (YOY) yellow perch energy allocation. Age-1+ fish (dashed lines) are tracked annually, while YOY yellow perch are tracked daily (solid lines). Diagram demonstrates model structure under baseline scenario (certain features are altered in other scenarios). For details, please see text.



Males mature at smaller sizes and younger ages than females (Diana and Salz 1990; Thayer et al. 2007). Males mature if their length exceeds 129 or 113 mm for age-1 and age-2, respectively. All age-3 males are assumed to be mature. Females mature if their

length exceeds 135, 130, and 125 mm for ages 2, 3, and 4, respectively. All age-5 females are assumed to be mature. Age-1+ growth rate of SL_t is assigned based on sex-specific von Bertalanffy growth functions (Table 1) as

Table 1. Information (values, units, and sources) regarding eco-genetic model parameters.

Parameter	Value	Unit	Source
Growth parameters for adults			
Male L_{∞}	272.0	mm	MDNR, unpublished data
Male K	0.184	year ⁻¹	MDNR, unpublished data
Female L_{∞}	307.0	mm	MDNR, unpublished data
Female K	0.333	year ⁻¹	MDNR, unpublished data
Survival parameters for adults			
Survival age-1	0.653		Thayer et al. 2007
Survival age-2	0.571		Thayer et al. 2007
Survival age-3	0.388		Thayer et al. 2007
Survival age-4	0.302		Thayer et al. 2007
Survival age-5	0.302		Thayer et al. 2007
Survival age-6	0.401		Thayer et al. 2007
Survival age-7	0.450		Thayer et al. 2007
Survival age-8	0.001		Thayer et al. 2007
Survival age-9	0.000		Thayer et al. 2007
Reproductive formulas			
Total eggs	138.2+187.1·W	Number	Brazo et al. 1975
Total milt	0.08·W	g	Le Cren 1951
Consumption parameters: $C = CA \cdot W^{CB} \cdot p \cdot f(T)$			
CA	0.51	g·g ⁻¹ ·day ⁻¹	Hanson et al. 1997
CB	-0.42		Hanson et al. 1997
CTO	29	°C	Hanson et al. 1997
CQ	2.3		Hanson et al. 1997
CTM	32	°C	Hanson et al. 1997
Respiration parameters: $R = RA \cdot W^{RB} \cdot f(T) \cdot ACT \cdot OxyConv$			
RA	0.0065	g·g ⁻¹ ·day ⁻¹	Hanson et al. 1997
RB	-0.2		Hanson et al. 1997
RQ	2.1		Hanson et al. 1997
RTO	32	°C	Hanson et al. 1997
RTM	35	°C	Hanson et al. 1997
ACT	4.4		Post 1990
OxyConv	13 560	J O ₂ ·g ⁻¹	
Egestion, excretion and specific dynamic action parameters (proportions)			
FA	0.15		Hanson et al. 1997
UA	0.15		Hanson et al. 1997
SDA	0.15		Hanson et al. 1997

Note: MDNR, Michigan Department of Natural Resources.

$$(3) \quad \Delta L_{i,t} = (L_{\infty} - L_{i,t}) \cdot (1 - e^{-K})$$

where $\Delta L_{i,t}$ is the growth increment (mm) of fish i in year t , L_{∞} is the asymptotic length of perch, $L_{i,t}$ is length at year t , and K is the perch growth parameter. Age-1+ total mass is determined by length-mass regressions for Saginaw Bay (Fiedler and Thomas 2006) as

$$(4) \quad M_{i,t} = 10^{-4.6} \cdot L_{i,t}^{2.8}$$

where $M_{i,t}$ is the total mass (g) (storage and structure) of the fish. Each SI is randomly assigned a survival rate (S_i , constrained from 0 to 1) from a normal distribution with an age-specific mean survival and an SD of 0.1 (Table 1; Thayer et al. 2007). As age-1+ fish are represented as SIs, the number of individuals represented by an adult SI decreases annually by $1 - S_i$.

Age-1+ reproduction

The total number of young fish produced annually by the adult population varies based on population-level egg production. Egg and milt production by mature females and males, respectively, are determined with mass-fecundity relationships (Table 1; Le Cren 1951; Brazo et al. 1975). Density-dependent survival of eggs to first-feeding larvae determines the number of new individuals that enter the model. Regardless of how many new individuals

enter the simulation in a year, they are divided evenly among 10 000 YOY SIs. Sex of new YOY SIs is randomly assigned ($P = 0.5$) and initial length after yolk-sac absorption is drawn from a normal distribution, $N(6.6 \text{ mm}, 0.2 \text{ mm})$ (Rose et al. 1999). Parentage of each new YOY SI is randomly assigned based on total individual female egg production (number of eggs per individual multiplied by the number of individuals represented by a female SI) and total individual male milt production (Le Cren 1951), such that SIs producing more eggs and more milt are more likely to parent offspring based on the proportion an SI contributes to the total milt or egg production).

Inheritance follows an allelic model such that parameter values are passed directly from parent to YOY: 50% of inherited parameter values from the mother and 50% of inherited parameter values from the father (e.g., Getz and Kaitala 1993; Wang and Höök 2009). Six inherited parameters (α_{1-6}) modify expected energy allocation throughout the growing season (see section on YOY energy allocation below). An SI's α_i expression is determined as the mean of two inherited parameters, one inherited from the SI's mother and one inherited from its father, for a total of 12 (2 alleles \times 6 genes) inherited values. The genetic structuring of energy allocation by young yellow perch is unknown. Our approach implicitly assumes that seasonal energy allocation is controlled by multiple genes and that expression can be captured via averaging of parental values. We chose a form requiring limited a priori definition of how energy allocation changes with season. For baseline simula-

tions, inheritance of individual parameters is assumed to be fully independent. While somewhat naïve, independent allelic models are advantageous as they require no assumption about genetic correlations (Dunlop et al. 2009). Ultimately, our focus is not on detailed modeling of genetic inheritance, but rather on evaluating differential selection for adaptively determined energy allocation patterns, which may be somewhat robust to the specific inheritance structuring (see below).

YOY hatch

To simulate temporal variability in hatching of yellow perch in Saginaw Bay, spawning occurs over a range of temperatures. Each YOY SI is randomly assigned a temperature at which it is assumed to be spawned (uniform distribution 7–11 °C; Rose et al. 1999). Time to hatch decreases with temperature and is determined with a modified cumulative development relationship from Rose et al. (1999) as

$$(5) \quad DV_d = \frac{1}{(145.7 + 2.56 \cdot T_d - 63.8 \cdot \ln T_d)}$$

where DV_d is an index of egg development duration and is calculated daily until the cumulative DV_d exceeds 1, when the YOY SI hatches. To simulate absorption of the yolk sac, the hatched SI does not feed for 3 days (Rose et al. 1999). Once feeding commences, daily consumption, respiration, mortality, and growth are simulated for each YOY SI on a daily basis.

YOY Wisconsin bioenergetics and growth

YOY SIs grow via a traditional Wisconsin bioenergetics subroutine (e.g., Kitchell et al. 1977; Post 1990; Hanson et al. 1997), which assumes the energy available for growth is a function of energy consumed less energy lost due to metabolic and waste processes:

$$(6) \quad G = C - R - F - U - SDA$$

where G is growth, C is consumption, R is respiration, F is egestion, U is excretion, and SDA is specific dynamic action, the effect of ingestion and assimilation on the production of body heat (all units are $\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$). Consumption (C) is modeled as a proportion (p) of temperature- and mass-dependent maximum consumption rate. Respiration is a temperature- and mass-dependent function, while egestion, excretion, and specific dynamic action are proportional to consumption. The above equation describes the general form of a Wisconsin bioenergetics model, while model subcomponents and specific parameter values are from Post (1990) and Hanson et al. (1997; see Table 1).

To account for compensatory density-dependent effects on growth, each SI's daily $p_{i,d}$ (proportion of maximum consumption) is calculated as a function of daily total YOY population biomass (B_d). The mean population proportion of maximum consumption, P_d , is defined as

$$(7) \quad P_d = 0.8 \cdot e^{-0.0000036 \cdot B_d}$$

where B_d is the total biomass (kg) of all YOY fish on day d (see Supplemental Material, Fig. 4S¹). This relationship was selected (1) to constrain values of p_d within ranges observed in other bioenergetics analyses (Kitchell et al. 1977), (2) to allow for realistic growth rates, and (3) to simulate compensatory density-dependent effects on growth as observed for age-0 yellow perch in Saginaw Bay (Ivan et al. 2011) by limiting consumption under large population sizes. Daily, individual proportions of maximum consump-

tion, $p_{i,d}$, are randomly ($P = 0.5$) drawn above or below P_d and are then assigned from one of two random uniform distributions: (i) $P_d \leq p_{i,d} \leq 1.0$ and (ii) $0 \leq p_{i,d} \leq P_d$. To simulate ontogenetic diet shifts, all individuals <30 mm feed on the same prey (zooplankton) with an energy density of $2300 \text{ J} \cdot \text{g}^{-1}$ (Schindler et al. 1971), while individuals >30 mm prey on chironomids with an energy density of $3100 \text{ J} \cdot \text{g}^{-1}$ (Schaeffer et al. 1999). Variation in growth therefore leads to variation in the timing of this ontogenetic diet shift.

YOY energy allocation

To simulate increases in mass and variable energy densities of individual fish, we model total individual mass as the sum of two tissue categories: structural and storage tissue. We assume that structural tissue is length-dependent, while storage tissue varies with size, individual feeding success, and seasonal energy allocation strategy. We assume that storage tissue has a high energy value ($6500 \text{ J} \cdot \text{g}^{-1}$), and structural tissue has a low energy value ($500 \text{ J} \cdot \text{g}^{-1}$), and we developed a length-based component of energy allocation to match observed energy densities of young perch from the Wisconsin bioenergetics manual (Hanson et al. 1997) and observed in Saginaw Bay (Pothoven et al. 2014; Roswell et al. 2014). Thus, while storage and structural tissues are conceptually constituted of high and low energy tissue types, respectively, we do not suppose that storage tissue is exclusively lipid or that structural tissue is exclusively bone.

There are two possible outcomes for daily growth. First, if the daily energy consumed is less than the energy expended because of respiration and other metabolic costs, growth in body mass is negative. If so, mass is lost only from storage tissue. Second, if the energy consumed is greater than the energy expended, mass is gained as either storage tissue or both storage and structural tissue.

Energy allocation to storage and structural tissue is size-dependent and potentially modified by seasonal adaptive controls. Hence, each day the proportion of excess energy allocated to storage tissue, $\rho_{i,d}$ (Höök et al. 2008), is determined as a function of both seasonal genetic values ($\beta_{i,j,d}$) and fish size ($X_{i,d}$; eq. 10) as

$$(8) \quad \rho_{i,d} = X_{i,d} + \beta_{i,j,d}$$

$\beta_{i,j,d}$ is the genetic component impacting energy allocation and varies from -0.2 to $+0.2$. This range allows for variation in energy allocation strategies within the range of energy densities observed for larval and YOY yellow perch (Forney 1971; Mason and Brandt 1996). $\beta_{i,j,d}$ is a linear combination of two inherited parameters (α_i and α_{i+1}):

$$(9) \quad \beta_{i,j,d} = k\alpha_{i,j} + (1 - k)\alpha_{i,j+1}$$

where $0 \leq k \leq 1$ and is the linear proportional contribution of genes $\alpha_{i,j}$ and $\alpha_{i,j+1}$ to individual i 's genetic expression on day d . The specific inherited parameters influencing energy allocation vary seasonally, and on one day of the year, each parameter has sole influence on energy allocation (i.e., $k = 1$; for graphical representation see Supplemental Material, Fig. 5S¹). For example, α_2 influences energy allocation from the day after hatch to day 211 and has sole influence on day 181. Other inherited parameters, $\alpha_{1,3-6}$, have sole influence on energy allocation on days hatch (α_1), 212 (α_3), 243 (α_4), 274 (α_5), and 305 (α_6), respectively. While it is arbitrary to select six inherited parameters, this seasonal separation allows α_{1-6} to be influenced by distinct seasonal selective pressures.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0197>.

Table 2. Summary of model simulations to consider: (A) differential inheritance structures; (B) alternative predation rates to consider differential selection pressures; and (C) alternative overwinter mortality rates to consider differential selection pressures.

(A) Inheritance structure simulations.			
	Independent	Linked	Linked with crossover
Baseline conditions	×	×	×
Switch from high to low mortality in year 100	×		×
Switch from low to high mortality in year 100	×		×
(B) Alternative predation pressure simulations.			
	Predation mortality		
Density-dependent	Low	Baseline	High
Density-independent	Low	Baseline	High
(C) Alternative winter mortality simulations.			
	Winter mortality		
Density-dependent	Low	Moderate	Harsh
Density-independent	Low	Moderate	Harsh

Length-based energy allocation is modeled as $X_{i,d}$, which is allowed to vary from 0.3 to 0.65 to constrain the total variation in energy allocation to 0.1–0.85. $X_{i,d}$ is determined as

$$(10) \quad X_{i,d} = 0.09 \cdot \ln(L_{i,d}) + 0.13$$

where $L_{i,d}$ is individual i 's length (mm) on day d (see Supplemental Material, Fig. 6S¹). This function was chosen as larger fish can store more lipids (Miranda and Hubbard 1994; Post and Parkinson 2001), and energy density tends to increase with fish size independent of season (e.g., Höök and Pothoven 2009; Pothoven et al. 2014). Each day, positive energy accrual is allocated first to storage until $\rho_{i,d}$ is reached. Then, remaining energy is allocated to both storage and structure such that $\rho_{i,d}$ is maintained. As structural tissue increases, so does length, based on adjusted length–mass regressions (Rose et al. 1999):

$$(11) \quad L_{i,d} = 61.56 \cdot ST_{i,d}^{0.36}$$

where $ST_{i,d}$ is the structural mass (g) of individual i on day d .

YOY mortality

Predation, starvation, and overwinter mortality affect survival of YOY SIs. Mortality due to predation and starvation is assessed daily, while overwinter survival is evaluated on the final day of the simulation year. The probability of dying due to predation ($Pred_{i,d}$) is

$$(12) \quad Pred_{i,d} = 1 - e^{-Z_{i,d}}$$

Daily instantaneous mortality rate, $Z_{i,d}$, is length-dependent and is determined as

$$(13) \quad Z_{i,d} = 0.4 \cdot e^{-L_{i,d} \cdot 0.06}$$

Length-dependent predation parameters were estimated to match observed mortality rates for newly hatched (Mason and Brandt 1996) and 40–50 mm larvae (Forney 1971) (see Supplemental Material, Fig. 7S¹). For each SI, the number of individuals predated is selected from a binomial distribution with $Pred_{i,d}$ as the probability and the number of individuals represented by the SI as the number of trials. Given this predation mortality framework, relative high energy allocation to structural tissue should decrease risk of predation mortality.

Starvation occurs when

$$(14) \quad R_{i,d} < S_{i,d}$$

where $R_{i,d}$ is the ratio of storage to total mass, and $S_{i,d}$ is defined as

$$(15) \quad S_{i,d} = 0.1 + 0.4 \cdot X_{i,d}$$

If $R_{i,d}$ is less than $S_{i,d}$, a random number (binomial, $P(n_{i,d}, S_{i,d})$) of individuals represented by an SI ($n_{i,d}$) experience starvation mortality (i.e., not all individuals represented by a SI are removed if the fish's storage capacity drops below the expected value). The probability of overwinter mortality ($Wint_i$) is evaluated after day 305 and is a function of a YOY SI's length and storage tissue such that larger individuals with higher energy densities are more likely to survive:

$$(16) \quad Wint_i = -173r_i^2 - 3r_i + 1$$

where r_i is the ratio of storage mass (g) to length (mm). We developed this relationship to ensure that fish > 80 mm did not experience overwinter mortality, while those < 50 mm experienced high winter mortality in keeping with findings in the literature (Post and Evans 1989). We incorporated storage into this equation so that fishes within the 50–80 mm size range ended up with a higher likelihood of surviving winter as storage mass increased (for graphical representation of this relationship, see Supplemental Material, Fig. 8S¹).

Model simulations

Selection for inherited traits through eco-genetic models may be sensitive to the inheritance structure employed (Dunlop et al. 2009). That is, inheritance structures may influence the speed and intensity of selection (resulting variance), and various inheritance structures may differentially respond to changes in selection pressures through the course of a selection trial. To evaluate if model results were robust to differential inheritance structures, we repeated base simulations with two additional inheritance structures: (i) linked allele inheritance and (ii) linked inheritance with crossover (Table 2). In linked inheritance scenarios, all parameters controlling energy allocation during the first year (α_1 – α_6) were inherited together (rather than independent, as in baseline simulations). Moreover, under linked inheritance we allowed offspring to express either the maternal or paternal parameters for energy allocation (rather than parental averaging, as employed in baseline simulations). Linked inheritance with crossover allowed for

random crossover between maternal and paternal alleles prior to the passage of genetic information to offspring. Crossover occurred with a 10% chance, and the location of the crossover was randomly selected. Moreover, to evaluate if inheritance structure influenced responsiveness to altered selection pressures, we explored model responses when varying size-dependent selection during the 200-year simulations. Specifically, we changed from high ($Z = 0.4e^{-0.05L}$) to low ($Z = 0.4e^{-0.08L}$) predation mortality and vice versa at year 100 for both linked and independent inheritance structures.

After model evaluation, we applied the model to explore the effects of various intensities of size-dependent predation mortality, overwinter mortality, and density-dependent growth on energy allocation of YOY yellow perch (Table 2). To this end, we performed the following simulations: (1) to understand the role of predation mortality on energy allocation, we simulated low ($Z = 0.4e^{-0.08L}$) and high ($Z = 0.4e^{-0.05L}$) predation mortality rates while keeping all other aspects of the model unchanged; (2) to evaluate how overwinter mortality structures energy allocation, we simulated low (decreasing the probability of winter mortality by 10%), moderate (increasing the probability of winter mortality by 10%), and harsh (increasing the probability of winter mortality by 25%) overwinter mortality while holding all other aspects of the model constant; (3) to determine the role of density-dependent growth on energy allocation, we performed simulations that allowed the mean feeding rate of YOY to either (i) be held constant ($P_d = 0.5$) or (ii) vary with YOY biomass. We performed different simulation types under both density-dependent and density-independent growth conditions (baseline, low predation, high predation, low overwinter mortality, moderate overwinter mortality, and high overwinter mortality). To account for stochastic effects, we replicated each type of simulation 10 times. We observed limited variation among replicates (see Results), justifying use of 10 replicates per simulation.

Results

Baseline simulations

Baseline simulations revealed transient behavior during the first 20 simulation years, followed by more stable dynamics (see Supplemental Material, Fig. 1S¹). At the end of the growing season in year 200, baseline simulations concluded with a population of approximately 5 million adults, an annual production of about 4 million age-0 fish, and mean YOY length and mass of 78 mm and 3.7 g, respectively. The mean (\pm SD) number of SIs in this simulation was $69\,968 \pm 298$.

There was strong selection on α parameters influencing energy allocation during early life. Parameters associated with energy allocation after hatch quickly evolved to negative α values (Fig. 2a). A negative α value signifies that a fish will allocate less energy to storage than initially expected based on length, as is the case for α_{1-3} . By examining changes in the range of α values, one can consider the relative selective pressure exerted on a parameter. The minimum values increased, while maximum values decreased for α_{1-2} (Fig. 2b), indicating strong selection on these parameters. Strong, stabilizing selection on α_1 controlling energy allocation is particularly noteworthy, especially considering that this parameter influences energy allocation for relatively few days as compared with α_{2-5} . In contrast, in baseline simulations mean α_{4-6} values remained closer to zero, and the range of values for α_{4-6} remained relatively large.

Effects of inheritance

Inheritance structure had little influence on population structure or the selection of genetic traits (Figs. 3a–3c; Supplemental Material, Figs. 2S and 3S¹). That is, final mean α values and the

trajectory of these values through the course of 200-year simulations were near identical among the three inheritance structures (Figs. 3a–3c; Supplemental Material, Figs. 2S and 3S¹). Incorporating abrupt changes in selection (i.e., switching from high to low and low to high mortality rates) using either linked or independent inheritance also resulted in very similar patterns in population structure and mean α values (Figs. 3d–3f; Supplemental Material, Figs. 2S and 3S¹).

Effects of differential selection pressures

The type and magnitude of selective pressure imposed on young yellow perch (predation versus overwinter mortality) had strong effects on population-level performance. Not surprisingly, lowering predation pressure resulted in increased abundance as compared with baseline simulations, while increasing predation pressure had the opposite effect (Figs. 4a and 4b). Individual length followed similar patterns, with smaller individuals occurring in the low predation scenario and larger individuals in the high predation scenario (Fig. 4c), while the energy density was higher in low predation scenarios (Fig. 4d). In general, with increasing winter severity, abundance and mean length decreased, while energy density increased.

Relaxation of density-dependent effects on energy allocation and potential growth resulted in increased population abundance for all scenarios (Fig. 4a), although removal of density-dependent effects in the low predation scenario led to large variation in YOY abundance (Fig. 4b). Mean YOY lengths increased after density-dependent effects were removed, especially for the low predation scenario (Fig. 4c). Similarly, energy density increased after removal of density-dependent constraints in all scenarios except the moderate and harsh overwinter mortality scenarios (Fig. 4d).

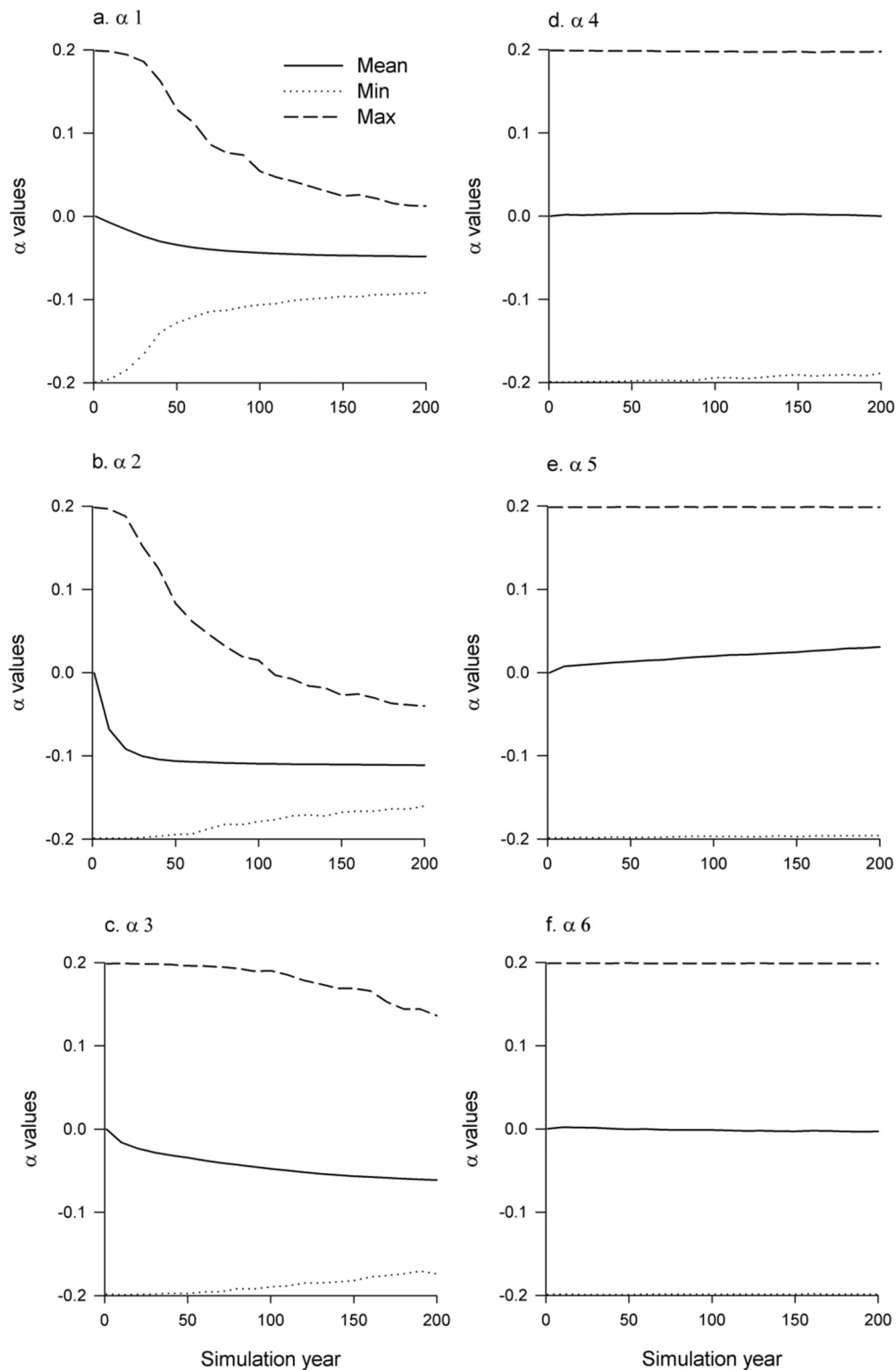
The impact of different selective pressures on parameters controlling energy allocation varied among scenarios as well as among each of the six inherited parameters. However, the type of selective pressure did not strongly impact energy allocation parameters early in ontogeny. Rather, in all simulations, energy allocation to structural tissue was prioritized during early ontogeny (i.e., mean α_1 and α_2 decreased; Figs. 5a and 5b). In addition, by the end of all 200-year simulations, the range and standard deviation of α_{1-2} were very low. Differences in energy allocation strategies among simulations were observed for parameters controlling energy allocation later in ontogeny (α_{3-6}). Specifically, simulated populations experiencing low predation pressure or moderate and harsh overwinter mortality allocated more energy to storage later in the growing season (Figs. 5c–5f). Further, the ranges of α_{3-6} values were constrained for low predation and high overwinter mortality scenarios. In particular, minimum α_{3-6} values increased, while maximum values remained near +0.2.

Relaxation of density-dependent control on growth did not drastically alter the final distribution of α values emerging under a given selective pressure, but subtle differences were apparent between density-dependent and density-independent simulations (Fig. 5). When considering all simulations concomitantly, relaxation of density-dependent growth tended to result in slightly lower mean α_{1-2} values, but led to differential responses of α_{3-6} values across simulation types, highlighting the interaction of ecological and environmental dynamics. Differences between mean α values in density-dependent versus density-independent simulations were particularly notable in mild, moderate, and harsh overwinter scenarios. Finally, simulations with density-independent growth generally resulted in less constricted ranges of α values, suggesting that selection on α values was less intense under density independence as compared with analogous simulations with density-dependent growth (Fig. 5).

Discussion

The early life history of animals is shaped by a complex set of interactions between inherited traits and environmental influ-

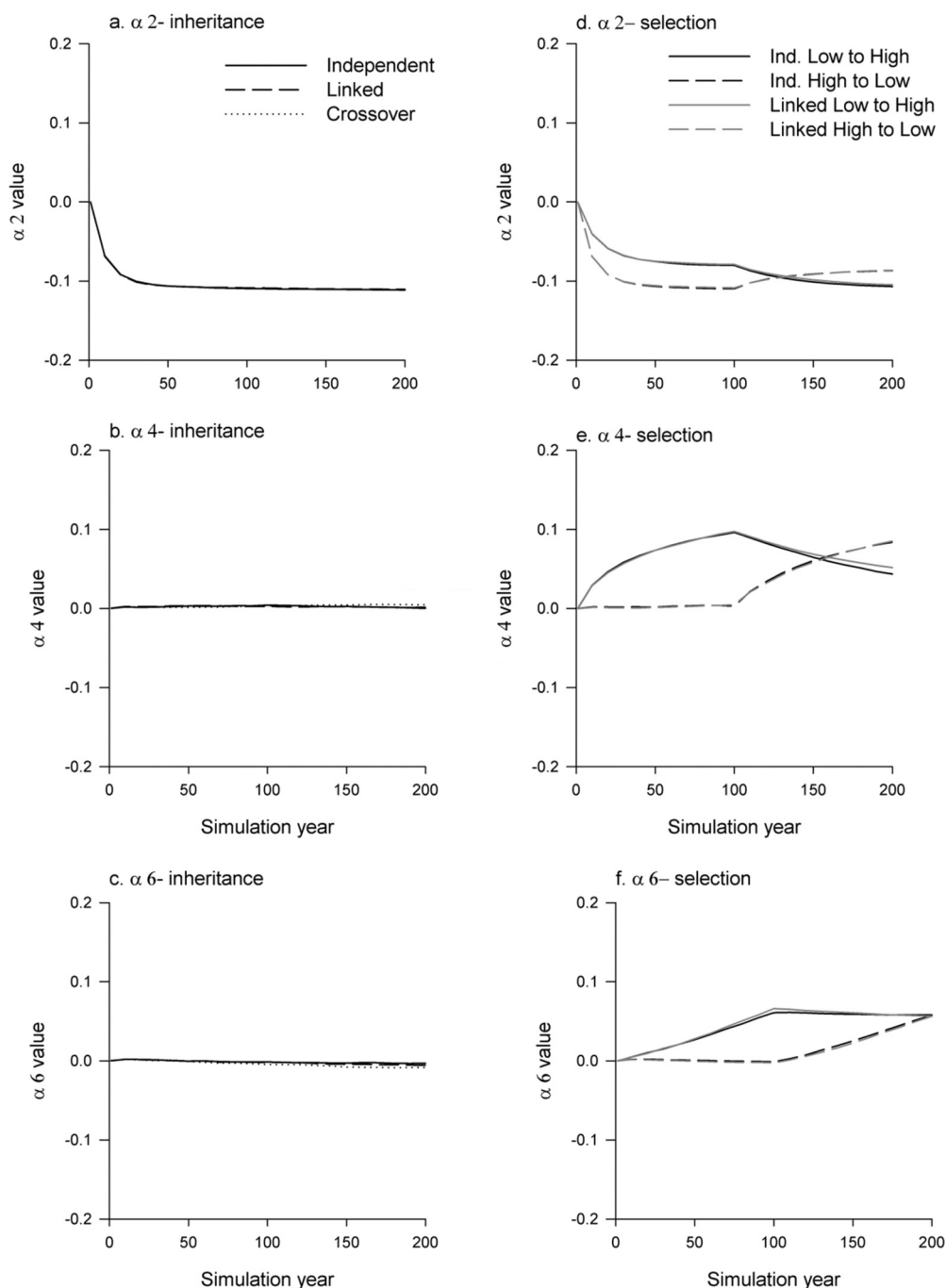
Fig. 2. Mean results of ten 200-year replicates of baseline simulations for mean, minimum, and maximum values for all six inherited parameters (α_{1-6} ; panels a–f) affecting energy allocation during the growing season. Parameter values initially varied uniformly between -0.2 and $+0.2$, and selective forces altered the distribution of values for α_{1-6} during the 200-year simulations. For clarity, minimum and maximum values in these plots represent the mean minimum and maximum values across the 10 simulations.



ences (Palkovacs 2003; Heino and Dieckmann 2008). Eco-genetic models provide a useful framework for elucidating environmental effects and underlying adaptive and plastic processes shaping various life history trait patterns (Dunlop et al. 2007, 2009; Wang and Höök 2009), including energy allocation of young ectotherms.

While many of the seasonal patterns of energy allocation emerging across simulations were consistent with past theoretical predictions and empirical analyses (see below), the eco-genetic model provides a framework to collectively consider the complex interactions among size-dependent predation pressure, risk of over-

Fig. 3. Effect of inheritance structure on selection for three representative energy allocation parameters, (a) α_2 , (b) α_4 , and (c) α_6 , for independent inheritance (base), linked parameters, and linked parameters with crossover and (d) α_2 , (e) α_4 , and (f) α_6 when varying predation mortality from low to high or high to low for independent inheritance and linked with crossover inheritance. Plots track the mean α parameter values across 10 simulations.



winter mortality, and individual growth rate on energy allocation in YOY ectotherms. Model results demonstrated (i) the relative strength of selective pressures during different ontogenetic stanzas and (ii) the potential for size-dependent mortality and growth rate to interactively influence energy allocation. Specifically, simulations collectively demonstrated that energy allocation exhibits strong, stabilizing selection during very early ontogeny, when small fish face intense, size-selective predation pressure. While such stabilizing selection on energy allocation diminishes later in the growing season, severe pressures (e.g., harsh overwinter mortality) strongly selects for inherited values affecting energy allo-

cation later in ontogeny. Moreover, plastic and adaptive processes interactively shape selection and expression of both genotypic and phenotypic components of energy allocation (e.g., interaction of size-dependent mortality and compensatory energy acquisition).

Rapid growth during early life promotes increased survival of young animals (e.g., Cowan et al. 1996; Houde 1997; Lindström 1999; Low and Pärt 2009), and energy allocation to structural tissue during early life facilitates such rapid growth. In fact, prioritized growth of low energy tissue at the expense of high energy tissue has been observed during early ontogeny in various fishes, including rainbow trout (*Oncorhynchus mykiss*) (Post and Parkinson

Fig. 4. Mean population values of the 10 simulations after 200 years of simulation for (a) mean age-1+ abundance, (b) mean YOY length (mm), (c) mean YOY abundance, and (d) mean energy density ($\text{J}\cdot\text{g}^{-1}$) at the end of the growing season (day = 305). Results are presented for 12 different types of simulations: baseline, low predation, high predation, mild winter mortality, moderate winter mortality, and harsh winter mortality (all scenarios were executed with (DD) and without (DI) density-dependent controls on growth). Each scenario was replicated 10 times, and plots depict 1.5 times the interquartile range of mean values of 10 simulations.

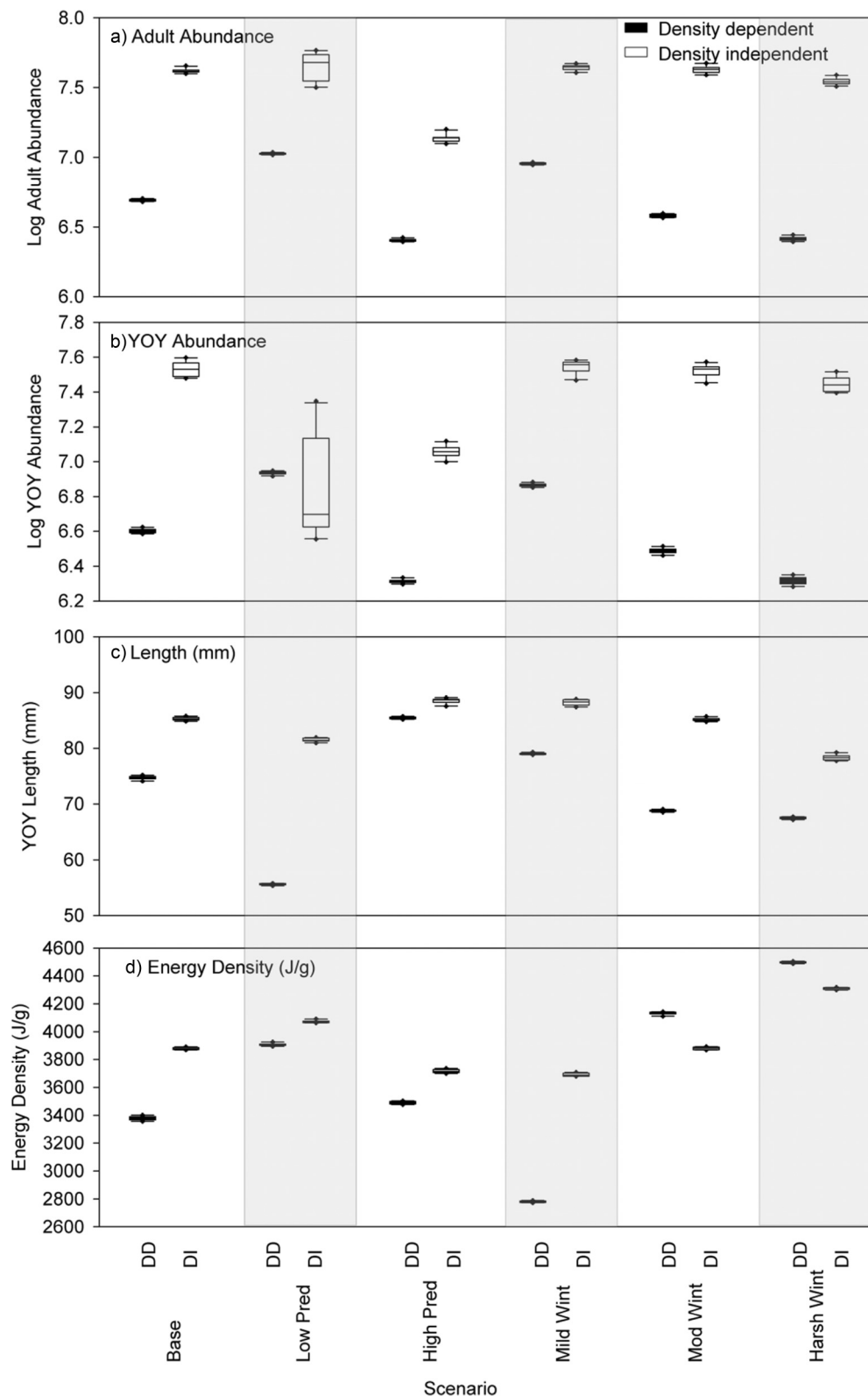
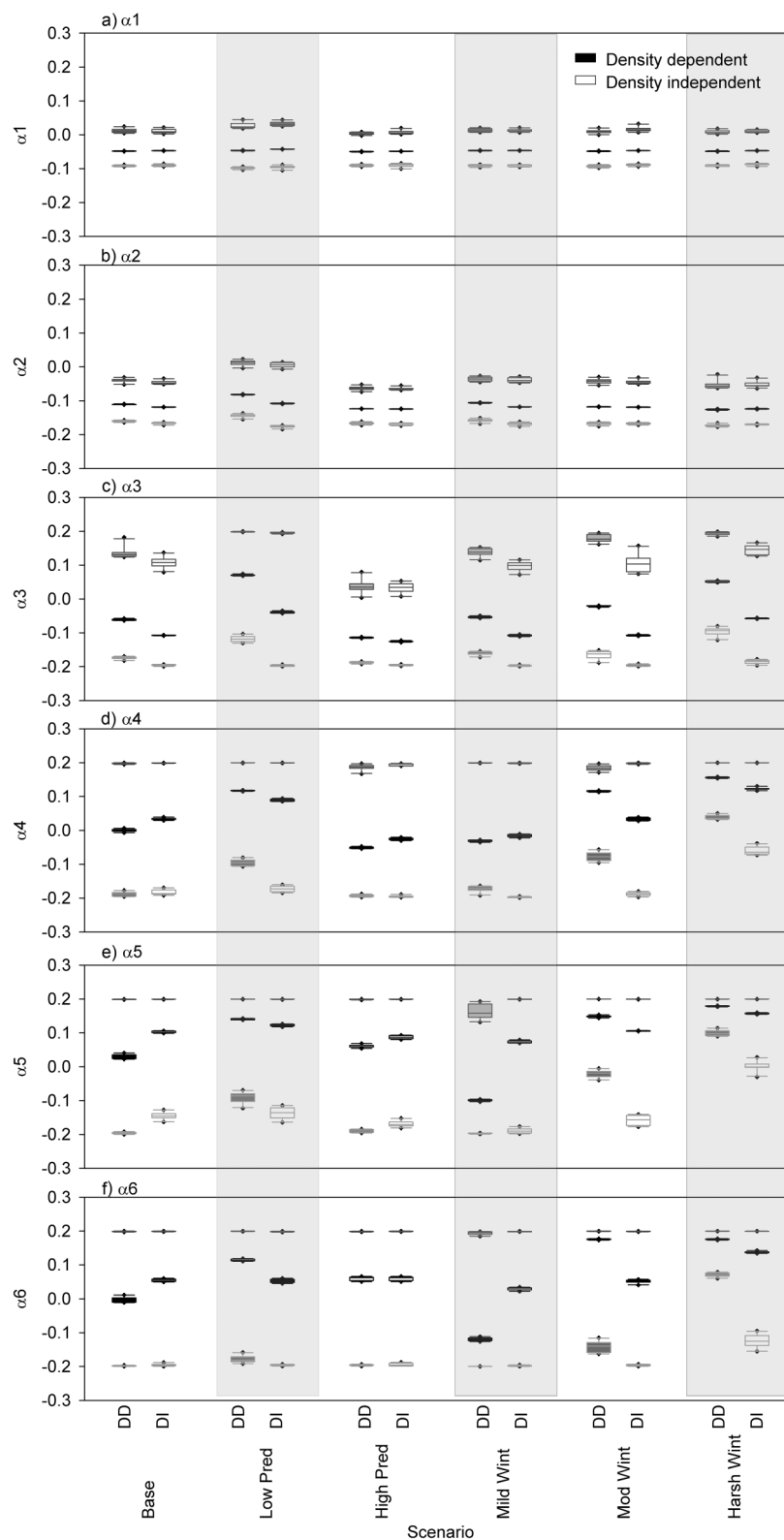


Fig. 5. Final mean of the mean, minimum, and maximum inherited parameter values (α_{1-6} ; panels a–f) at the end of the growing season (day 305) in simulation year 200. Results are presented for 12 different types of simulations: baseline, low predation, high predation, mild winter mortality, moderate winter mortality, and harsh winter mortality (all scenarios were executed with (DD) and without (DI) density-dependent controls on growth). Each scenario was replicated 10 times, and plots depict 1.5 times the interquartile range across these 10 simulations for mean values (black box plots with intermediate values), maximum values (gray box plots with relatively high values), and minimum values (gray box plots with relatively low values).



2001; Biro et al. 2005), largemouth bass (Miranda and Hubbard 1994), striped bass (Hurst and Conover 2003), and alewives (*Alosa pseudoharengus*) (Höök and Pothoven 2009). The importance of size-dependent survival during early life of temperate fishes was exemplified in all of our model simulations by the rapid selection of negative mean values for parameters α_{1-2} , such that YOY fish allocated energy to structural tissue, spurring rapid growth in length. The variation associated with these parameters also rapidly decreased, suggesting that parameters relating to energy allocation early in development of YOY fishes are tightly constrained by size-dependent predation pressure and other mortality sources. If young animals do not survive during very early life (e.g., larval stage), energy allocation strategies during later life become irrelevant. To this point, while the range of α_{1-2} values became quite constrained in all simulations, the range of α_{3-6} values remained relatively high throughout most simulations. Thus, our simulations suggest that the selective pressures favoring rapid growth in size during very early life are greater than subsequent selective pressures on energy allocation as winter approaches. Nonetheless, selective pressures clearly influence energy allocation during later life, as mean α_{3-6} values differed among simulations.

Influence of overwinter mortality

In general, risk of overwinter mortality is greater for smaller individuals. Storage capacity and mass-specific metabolism (Kleiber 1932; Schultz and Conover 1999; Brown et al. 2004) both scale with size such that smaller animals tend to deplete energy reserves at a faster rate than larger individuals (Biro et al. 2004; Garvey et al. 2004; Borchert et al. 2007; Huss et al. 2008). Depleted energy stores not only cause young animals to die from starvation, but may also increase their susceptibility to disease (Adams 1999) and lead to risky foraging behavior, exacerbating potential predation-based mortality during winter or early spring (Biro et al. 2005). Therefore, small animals benefit disproportionately by increasing size and increasing storage tissue. In our simulations, prioritized allocation of energy to storage tissue occurred earlier and was more extreme in simulations with high risk of overwinter mortality, as this strategy led to a greater probability of survival through winter. Further, this strategy appears in part to represent an adaptive response to high winter mortality, because faster growth through relaxation of compensatory density-dependent energy acquisition did not qualitatively alter energy allocation parameters.

Our findings that degree of winter severity should impact adaptive energy allocation strategies of YOY temperate fishes are generally consistent with observations from field, laboratory, and modelling studies. Size- and energy-dependent overwinter mortality affects fish populations in northern climates (Post and Evans 1989; Mogensén and Post 2012) and likely contributes to latitudinal differences in energy allocation strategies of fishes, including Atlantic salmon (Berg et al. 2009), brown trout (*Salmo trutta*) (Álvarez et al. 2006), and Atlantic silverside (*Menidia menidia*) (Schultz and Conover 1997). Likewise, within-population variation in winter survival has been shown to be dependent on individual size and winter duration in fishes such as rainbow trout (Biro et al. 2004; Mogensén and Post 2012) and yellow perch (Post and Evans 1989). Temperate fish populations that reach a relatively large size during the first year of life should not be as vulnerable to overwinter mortality as those that are smaller in late fall. For example, studies by Post and Evans (1989) and Fitzgerald et al. (2004) suggest that yellow perch equivalent in size to the mean observed in our baseline simulations (mean = 76 mm) should be relatively safe from overwinter mortality. In contrast, in our high overwinter mortality simulations with relatively rapid, density-independent growth, selection nonetheless strongly favored allocation of energy to storage tissues. Moreover, Huss et al. (2008) found that high growth rates late in the season, regardless of size, could result in increased survival of YOY Eurasian perch (*Perca fluviatilis*). These authors noted that increased survival was related to posi-

tive growth-dependent increases in energy allocation to storage tissue, a result similar to our finding. As such, size, season, and growth rates interact to determine energy allocation strategies in temperate fishes (Hurst and Conover 2003; Garvey et al. 2004; Huss et al. 2008; Mogensén and Post 2012; Jacobs et al. 2012).

Interactive effects of size-dependent mortality and compensatory growth

Prioritized allocation of energy to storage tissue also occurred earlier and was more extreme in simulations with low predation pressure. In comparison with high overwinter mortality scenarios, energy allocation under low predation pressure seems to represent a somewhat more complex feedback. On the one hand, low predation pressure decreases the risk of size-dependent predation mortality, thereby (i) reducing the selective pressure to grow large to avoid predation, (ii) increasing the relative selective importance of overwinter mortality, and (iii) favoring energy allocation to storage tissue. On the other hand, low predation pressure increases survival and overall population abundance, thereby leading to slower growth rates and smaller individual sizes by the end of the growing season, which also increases the risk of overwinter mortality and favors allocation of energy to storage tissue. In simulations with low predation pressure and no density-dependent controls on energy acquisition, α_{4-6} values were lower than in analogous simulations with density-dependent effects. This indicates weaker selection for increased allocation to storage tissues under the density-independent scenario. Hence, compensatory density-dependent effects on energy acquisition constitute an important dynamic by which magnitude of predation pressure can influence adaptive energy allocation. Such complex feedbacks make a priori predictions difficult and highlight the utility of eco-genetic models, which allow for the complex feedbacks among density, growth, and survival that are lacking in more traditional modeling approaches.

While the effects of predation pressure on energy allocation can be quite complex, it is nonetheless evident that the magnitude of predation pressure imparts selective pressure on energy allocation. For example, consider α_3 , which affects energy allocation during the middle of the growing season. Selection on this parameter is not as strong as selection on α_{1-2} , which control energy allocation during very early life, and α_3 does not respond as strongly to risk of overwinter mortality as α_6 . However, mean α_3 values were lowest in simulations with high predation pressure (with either density-dependent or density-independent growth). Further, in density-independent simulations, α_3 values were lowest under high predation pressure, intermediate under baseline predation pressure, and highest under low predation pressure. Thus, even when compensatory effects do not impact individual rates of energy acquisition, predation pressure still selects for differential energy allocation strategies. In fact, past studies have also demonstrated an effect of predation pressure on energy allocation strategies. Biro et al. (2005) found that young rainbow trout allocated energy to structure in summer but switched to allocating energy to storage in the fall. Further, these authors found that size-dependent predation on YOY trout selects for increased risk-taking and energy allocation to structure early in ontogeny. Once trout had grown sufficiently large to minimize predation risk, overwinter mortality became the stronger selective force, and trout greater than 50 mm began allocating much of their excess energy to storage tissue. These results are similar to our study in that fish experiencing high predation pressure select for growth in length over storage during early ontogeny.

The two-way feedback between size and energy allocation leads to interesting dynamics. In simulations with slow growth and small sizes, risk for overwinter mortality is elevated, and hence there is selection for prioritized growth of storage tissues. However, allocation of energy to storage tissues reduces growth rates. For example, owing to a trade-off between growth of storage and

structural tissues, density-independent simulations with low predation pressure or high overwinter mortality produce relatively short individuals. Simulated populations with smaller mean sizes prior to winter onset tended to prioritize allocation of energy to storage tissues early and were relatively heavy per unit length. In general, because of allometric energy allocation, energy densities of smaller individuals are relatively low (i.e., they allocate relatively more energy to structure; Post and Parkinson 2001; Garvey and Marschall 2003; Garvey et al. 2004; Jacobs et al. 2012). When comparing across populations and adjusting for size, however, young fish from higher latitudes tend to accumulate lipids more rapidly and become relatively heavy per unit length (as seen in Atlantic silversides; Schultz and Conover 1997). Moreover, such fish may be more likely to replace lipids lost after starvation before continuing to grow in length in the winter (as observed in Atlantic salmon; Metcalfe et al. 2002).

Plastic versus adaptive responses

Teasing apart plastic versus adaptive responses can be difficult. Our model allowed us to compare the expression of phenotypic traits (i.e., length and energy density) with genetic expressions to consider the relative influences of adaptive versus plastic responses. In general, genetic changes resulted in corresponding changes in life history traits (i.e., higher α values led to higher energy density). However, this was not always the case. For example, consider low predation scenarios with and without density dependence. Simulations with density dependence resulted in relatively high α values, but relatively low energy density. These apparent discrepancies were likely mediated by differences in growth rates and final sizes (i.e., density-independent scenarios resulted in much larger fishes).

Collectively, model simulations reveal how size-dependent selection pressures and density-dependent growth can synergistically affect energy allocation of young animals. Comparisons across different types of simulations reveal that while two differential selective pressures may select for divergent inherited parameters, such divergences may not be apparent through inspection of mean individual trait expression (length, mass, and energy density or storage/total tissue). For example, under density independence, various mortality scenarios (baseline, low predation, high predation, mild winter, and moderate winter) result in similar final mean lengths, even though evolved inherited parameters are quite distinct among mortality scenarios (consider α_4). Similarly, two selective pressures can lead to differential trait expression without differentially selecting for distinct inherited parameters (e.g., similar energy densities or storage to total mass ratios despite distinct evolved α values). Emergence of such veiled patterns demonstrates the utility of eco-genetic models for generating and evaluating hypotheses that cannot be readily addressed through empirical studies. Moreover, these types of veiled patterns may have implications for (i) managers intending on stocking organisms that have evolved under a certain set of selective forces into areas with highly divergent selective forces and (ii) researchers aiming to anticipate how a certain population may respond to future selective pressures.

Inferences from eco-genetic models

Yellow perch in Saginaw Bay are currently experiencing low population numbers, and recent studies have shown that overwinter mortality in YOY may play a role in population decline (Ivan et al. 2011; Roswell et al. 2014). Our model was not calibrated to recent (2009–2011) Saginaw Bay yellow perch energy allocation patterns presented by Pothoven et al. (2014) and Roswell et al. (2014). Nonetheless, baseline simulations, calibrated to historic Saginaw Bay yellow perch growth patterns (e.g., Ivan et al. 2011) show similar early life energy allocation patterns as those documented by Pothoven et al. (2014) and Roswell et al. (2014). Our model scenarios show decreased perch populations (i) when den-

sity dependence leads to slow growth heading into winter; (ii) when harsh winters occur, and (iii) under heavy predation pressure. These results are generally consistent with yellow perch populations in Saginaw Bay (e.g., in 2003, high production of age-0 fish produced small age-0 fish heading into winter but resulted in low 2004 fall age-1 fish; Ivan et al. 2011).

Despite some similar patterns between our model simulations and observations for yellow perch in Saginaw Bay, we suggest that direct comparisons between our model and empirical observations should be qualitative in nature. Similar to other eco-genetic models (e.g., Wang and Höök 2009), our model includes several processes and parameter values with weak empirical evidence. For example, the genetic structuring of energy allocation in young yellow perch is largely unknown. We used a flexible modeling approach to allow seasonal energy allocation to evolve with limited a priori definition of form of such seasonal patterns. It is possible that true genetic structuring of energy allocation by young yellow perch is far less flexible and could constrain energy allocation patterns. Without understanding true genetic structuring of energy allocation, future applications of this or similar models could consider the consequences of different types of genetic structuring (e.g., increasing or decreasing the number of α parameters or modeling energy allocation as a linear function of day of year, controlled by a heritable slope and intercept).

While our model includes several aspects underlying early life energy acquisition and allocation, as with any model it is an abstraction of reality, and there is a limit to the number of processes that we can consider. Several processes and trade-offs that we did not consider could have affected model behavior. For example, several past studies have pointed to a trade-off between foraging (fast growth) and risk of predation for small ectotherms (Lima 1998; Garvey et al. 2004; Biro et al. 2005; Mogensen and Post 2012). As a young fish forages and subsequently grows, there are likely interacting effects on mortality. An actively foraging fish may be immediately more susceptible to predation, but as a fish becomes larger, increased size should decrease risk of predation mortality (e.g., Cowan et al. 1996; Garvey et al. 2004). We incorporate the second effect and essentially assume that the benefit of becoming larger outweighs the risk of foraging. However, this assumption could be altered and future applications could incorporate risk of foraging as an additional factor influencing energy acquisition or allocation. Similarly, we do not explicitly track a dynamic prey base, but rather assume that energy acquisition is under compensatory density-dependent control (see eq. 6). While it is unclear that explicit tracking of a prey base would fundamentally change energy allocation patterns, it is plausible that a dynamic prey base could lead to more variable energy acquisition. Finally, we selected six genetic traits to control energy allocation to correspond to the roughly 6 months of growth YOY fish have prior to winter onset. The number of genetic traits controlling energy allocation is unknown; as such, any number of controllers could be selected, and the number of genetic controls on energy allocation could impact our model results. Future applications of our model could consider the consequences of such variation on energy allocation patterns.

In summary, the study presented herein demonstrates how an eco-genetic modeling approach can be used to explore a complex trait trade-off influenced by both plastic and adaptive processes. Again, we suggest that similar to other eco-genetic models, it is not appropriate to use this model to make precise predictions of population dynamics or genetically determined trait expression. Rather, we believe it is appropriate to use the model analogous to a genetic algorithm to qualitatively consider patterns under different selection pressures. While model results were generally consistent with past empirical studies of energy allocation, to our knowledge, no past study has simultaneously considered as many selective pressures acting on young fish energy allocation and over as long of a time as our model. Tracking of both the mean and

variance of genetic parameters allowed for comparison of selective pressures both in terms of direction (mean) and strength (variance) acting on genetic traits. Thereby, the model provides a framework for evaluating multiple effects of various selective pressures on both genotypic and phenotypic expression of early life energy allocation.

Acknowledgements

This work was funded by a grant from the National Oceanic and Atmospheric Administration's (NOAA) Center for Sponsored Coastal Ocean Research. We thank Carolyn Foley and Daisuke Goto for comments on a previous version of this manuscript, as well as three anonymous reviewers of an earlier draft. This is a NOAA Great Lakes Environmental Research Laboratory contribution No. 1760 and a Michigan State Quantitative Fisheries Center contribution No. 2015-11. Author contributions: TOH developed the study idea and hypothesis and substantially edited and improved the manuscript. LNI developed the model, performed analyses, and wrote the manuscript.

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